

KENTRIODON OBSCURUS (KELLOGG, 1931), A FOSSIL DOLPHIN (MAMMALIA: KENTRIODONTIDAE) FROM THE MIOCENE SHARKTOOTH HILL BONEBED IN CALIFORNIA

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ABSTRACT. The fossil odontocete genus *Kentriodon* Kellogg, 1927, is the type genus of the delphinoid family Kentriodontidae, a family which has no living representatives. The genus *Kentriodon* has previously included only one named species, a small dolphin called *Kentriodon pernix* Kellogg, 1927, from the Middle Miocene Calvert Formation in Maryland and Virginia on the east coast of North America. Some bones from Japan and California have previously been tentatively referred to the genus. We have concluded that the species *Grypolithax obscura* Kellogg, 1931, heretofore known only by isolated periotics from the Middle Miocene Sharktooth Hill Bonebed in California, belongs in *Kentriodon*. The genus *Grypolithax* Kellogg, 1931, is therefore a junior synonym of *Kentriodon* Kellogg, 1927. A second species named on isolated periotics from the Sharktooth Hill Bonebed, *Grypolithax pavidus* Kellogg, 1931, is a synonym of *G. obscura*. The appropriate binomen for the species is *Kentriodon obscurus* (Kellogg, 1931). We assign to this species a partial skull and additional isolated periotics from the same bonebed.

Other isolated periotics from rocks stratigraphically below the Sharktooth Hill Bonebed in California resemble those of *Kentriodon* spp. and a closely related kentriodontid, *Delphinodon dividum* True, 1912, which was also originally described from the Calvert Formation. Some of these have been referred to in previous literature, but are illustrated and described here for the first time.

These newly reported specimens from California reinforce some previous correlations between the upper part of the Round Mountain Silt in California and the Calvert Formation in Maryland and Virginia. They also provide additional indications of a general pattern of generic cosmopolitanism and specific endemism among the Miocene odontocetes of the North Atlantic and North Pacific Oceans.

INTRODUCTION

Fossil odontocetes of the genus *Kentriodon* Kellogg, 1927, are small Miocene dolphins in the extinct family Kentriodontidae. Kellogg (1928:33, 68) assigned the genus to the family Delphinidae. Slijper later (1936:556) named a new subfamily Kentriodontinae, which he placed within the Delphinidae, to include *Kentriodon* as well as *Delphinodon dividum* True, 1912, another Miocene dolphin. Barnes (1978) altered the context and rank of Slijper's family group name by recognizing the family Kentriodontidae within the superfamily Delphinoidea. He recognized three subfamilies (Kampholophinae, Kentriodontinae, and Lophocetinae) within the Kentriodontidae, and the species included in this family are now known by described fossils from Europe, Japan, New Zealand, and both the east and west coasts of North America. The importance of this family and its relationships to some other odontocete families was commented on by Barnes. He stated that kentriodontids might comprise the group from which other living families of delphinoids, including modern dolphins in the Delphinidae, have evolved, and they might also be expected to occur widely in rocks of appropriate age

around the world. Our interests in delphinoid evolution and in the Middle Miocene cetaceans in the Sharktooth Hill Local Fauna in California have led us to the present study.

The type species of *Kentriodon*, *K. pernix* Kellogg, 1927, was named on the basis of two skulls, one of which was collected with earbones and an articulated partial postcranial skeleton (the holotype), of Middle Miocene age from the Calvert Formation in Maryland. Until the present study, this genus has had assigned to it only this one named species, however, some references in the paleontologic literature have suggested the former presence of the genus in the North Pacific Ocean. The genus *Kentriodon* was questionably identified from Miocene rocks in Japan by Shikama, Hasegawa, and Otsuka (1973; also cited in Okazaki, 1976:25), but specimens documenting this identification have not been described. Barnes (1976:326) identified as cf. *Kentriodon* and as a related kentriodontid, cf. *Delphinodon dividum* True, 1912, some isolated periotics of early Middle Miocene age from the lower part of the Round Mountain Silt in Kern County, California. The source of these is stratigraphically lower than the Middle Miocene Sharktooth Hill Bonebed. Other kentriodontid genera have been recognized based on skulls from Miocene rocks in Europe and California (Kellogg, 1925:4-6; Barnes, 1976, 1978), and from late Oligocene rocks in New Zealand (Fordyce, 1980:328).

Kellogg (1931) prepared a preliminary description of the mammals from the Sharktooth Hill Bonebed that comprise a part of what we now call the Sharktooth Hill Local Fauna (Mitchell, 1965:33; Mitchell and Tedford, 1973: fig. 3; Barnes, 1976:326-327). In this study, Kellogg named ten new species of small odontocetes based solely on isolated periotics from the bonebed. For many years the true identities and relationships of these species have remained unknown. The problem of disparate skeletal parts has in some instances precluded objective morphologic and taxonomic comparisons between the odontocetes from the Sharktooth Hill Bonebed and other taxa (even some studied by Kellogg himself) known by skulls and skeletons from elsewhere in the world. For example, Barnes (1978) showed that *Liolithax kernensis* Kellogg, 1931, from the Sharktooth Hill Bonebed is congeneric with *Lophocetus pappus* Kellogg, 1955, from the Calvert Formation in Maryland.

In the present study, we show that *Grypolithax obscura* Kellogg, 1931, from the Sharktooth Hill Bonebed is conge-

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neric with *Kentriodon pernix*. Another species Kellogg named from the bonebed, *G. pavida* Kellogg, 1931, is synonymous with *G. obscura* and the properly emended binomen for the species from California is *Kentriodon obscurus* (Kellogg, 1931). We refer a partial skull and several more isolated periotics from the Sharktooth Hill Bonebed to *K. obscurus*, and with these we have been able to more fully characterize the species and compare it with *K. pernix*. We also describe and illustrate the specimens of kentriodontids that Barnes (1976) mentioned from stratigraphically lower levels of the Round Mountain Silt in California.

MATERIALS AND METHODS

INSTITUTIONAL ACRONYMS

The specimens examined in the course of this study are in the collections of the following scientific institutions: California Academy of Sciences, San Francisco, California (CAS); Natural History Museum of Los Angeles County, Los Angeles, California (LACM); University of California Museum of Paleontology, Berkeley, California (UCMP); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Institutional locality numbers are given for specimens where appropriate. Qualified investigators may obtain precise locality information by contacting the appropriate institutions.

COMPARATIVE MATERIAL

We have made extensive reference to and comparisons with the type species of *Kentriodon*, *K. pernix* from the Middle Miocene Calvert Formation in Maryland. We believe that the holotype (USNM 8060) of *K. pernix*, which was collected from Zone 5 relatively low in the Calvert Formation, and Kellogg's original (1927a) published referred skull (USNM 10670) from Zone 3 slightly lower in the formation, represent the same species. These are the only skulls of *K. pernix* that have been described in the literature.

We have identified one other small skull (USNM 21027) as *K. pernix*. It was found at Plum Point, Maryland, where Zone 6 of the Calvert Formation (also relatively low in the rock unit) is exposed at sea level (see Clark, Shattuck, and Dall, 1904: pl. 5). These three specimens, therefore, comprise our current concept of the species, but provide only limited information on individual and ontogenetic variation within the species.

There are several additional fossils of *Kentriodon* from the Calvert Formation in Virginia and Maryland in the USNM collections that are undescribed in the scientific literature. Some of these are significantly different from both the holotype and referred specimens of *K. pernix*. Most are from zones higher in the Calvert Formation, and are therefore geologically younger than the holotype and referred specimens of *K. pernix*. We conclude that one or more species in addition to *K. pernix* are represented by these additional specimens, but a detailed variability and taxonomic study of *Kentriodon* from the Calvert Formation is beyond the scope of the present study. In the absence of such a study of these

other *Kentriodon* specimens, we made some observations on them that have influenced our diagnoses and comparisons. Additionally, we have illustrated some of the periotics (Figs. 8–9) to demonstrate variable characters within the genus.

TERMINOLOGY

The morphology of a kentriodontid periotic is shown in Fig. 1. The terminology used is derived or adapted from Denker (1902), Boenninghaus (1904), and Kellogg (1928). Cranial terminology is derived from Kellogg (1927a) and Fraser and Purves (1960). Where we employ family group names with different rank than originally proposed, we cite the author of the emended rank following the original author.

Statistical analysis follows Simpson, Roe, and Lewontin (1960).

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Delphinoidea (Gray, 1821)
Flower, 1864

Family Kentriodontidae (Slijper, 1936)
Barnes, 1978

Kentriodontinae Slijper, 1936:556; as a subfamily of the family Delphinidae.

Kentriodontidae. Slijper, 1958: label in fig. 36, emended rank without explanation in text.

Kentriodontidae. Barnes, 1978:3; emended rank, as a family of the superfamily Delphinoidea.

DISCUSSION. Barnes (1978) stated that a lack of fossae in bones of the basicranium, reflecting a presumed lack of extensive development of air sinuses of the middle ear air sinus system, was a characteristic feature of the family Kentriodontidae. Aside from the usual, primitive odontocete combination of peribullary and pterygoid air sinuses, we find in *Kentriodon* spp. osteological evidence only for a middle sinus adjacent to the glenoid fossa and for a postorbital lobe of the pterygoid sinus. We find no fossae that would provide evidence for a posterior sinus in the exoccipital, for any sinuses in the basioccipital or above the optic nerve (as in phocoenids), for a large orbital lobe, or for an anterior sinus extending onto the posterior part of the palate. These are all locations where various modern odontocetes have been shown to have air sinuses in their skulls (Fraser and Purves, 1960). The fossa for the lobe of the pterygoid sinus within the pterygoid hamulus is characteristically small in Kentriodontidae compared with Delphinidae, Phocoenidae, Ziphiidae or Physteridae. No fossil kentriodontid skull has yet been described with an ossified pterygoid hamulus flooring the ventral surface of this sinus as in modern delphinids, phocoenids, and monodontids, and it cannot be determined from the

specimens presently available whether or not these animals had an incomplete or non-ossified hamulus as in modern platanistoid dolphins (see Fraser and Purves, 1960).

Subfamily Kentriodontinae Slijper, 1936

Kentriodontinae Slijper, 1936:556; as a subfamily of the family Delphinidae.

Kentriodontinae. Barnes, 1978:24; emended context, as a subfamily of the family Kentriodontidae.

Kentriodon Kellogg, 1927

Kentriodon Kellogg, 1927a:4.

Grypolithax Kellogg, 1931:393.

EMENDED DIAGNOSIS OF GENUS. A genus of the subfamily Kentriodontinae differing from *Delphinodon divi-dum* by having a skull with a longer rostrum, the mesorostral gutter not roofed over by the premaxillae at the anterior end, a more concave lateral margin of the supraorbital process, palatal surfaces of maxillae more transversely convex, and a fossa for the postorbital lobe of the pterygoid air sinus on the ventral surface of the frontal; differing from *Leptodelphis*, *Microphocaena*, *Pithanodelphis*, and *Sarmatodelphis* by having a more convex lateral margin of the supraorbital process, flat rather than bulbous or convex nasal bones, and more widely separated posterior ends of the maxillae at the cranial vertex with a concomitantly wider exposure of the frontals, differing from *Leptodelphis* and *Pithanodelphis* by having a less elevated cranial vertex; and differing from *Liolithax*, *Delphinodon*, *Lophocetus*, and perhaps other described genera of Kentriodontidae by having the anterior-most premaxillary tooth on each side elongated into a small tusk and pointing anteriorly from the tip of the rostrum.

TYPE SPECIES. *Kentriodon pernix* Kellogg, 1927; type by original monotypy.

INCLUDED SPECIES. *Kentriodon pernix* Kellogg, 1927; and *Kentriodon obscurus* (Kellogg, 1931), new combination.

Kentriodon obscurus (Kellogg, 1931), new combination

Figures 2–7, 8d–t, 9d–t, 13b, 14b

Grypolithax obscura Kellogg, 1931:394.

Grypolithax pavidus Kellogg, 1931:396.

EMENDED DIAGNOSIS OF SPECIES. A species of *Kentriodon* characterized by and differing from *K. pernix* by having skull with vertically short postorbital process of frontal, posterior part of alveolar row curved medially on palatal surface instead of extending along lateral margin of rostrum, posterior maxillary alveoli directed more laterally than ventrally, lateral margin of maxilla adjacent to posterior part of alveolar row thickened and squared off instead of being thin and rounded, alveoli for maxillary teeth averaging 1.5 mm in diameter instead of 3 mm, antorbital notch narrow and directed anteriorly instead of wide and directed anterolaterally, supraorbital process of frontal thicker and more arched,

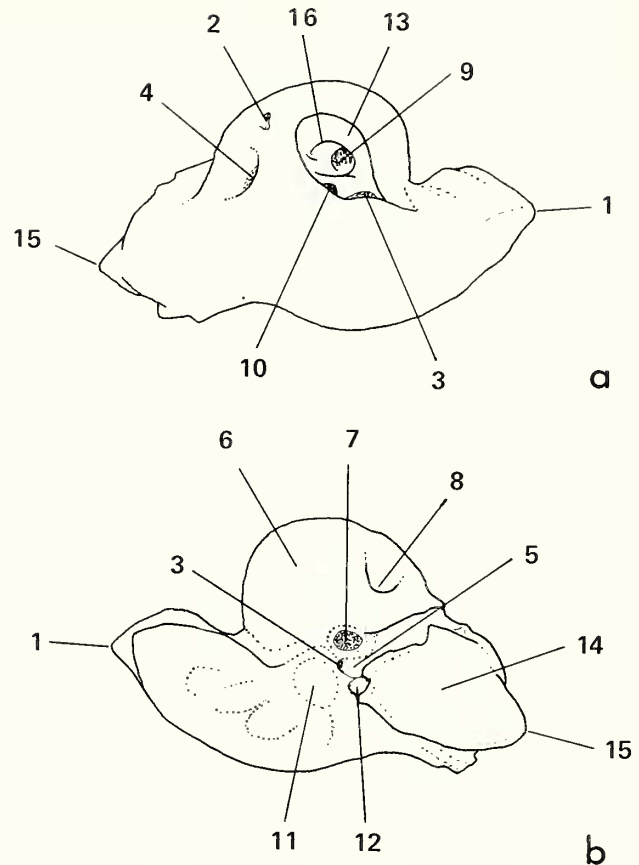


Figure 1. Right periotic of a kentriodontid, cf. *Kentriodon* sp., UCMP 83605, with anatomical structures labeled; **a**, cerebral or dorsal view; **b**, tympanic or ventral view, natural size. 1—anterior process, 2—aquaeductus cochleae, 3—aquaeductus Fallopii, 4—aquaeductus vestibuli, 5—canal for facial nerve, 6—cochlear portion, 7—fenestra ovalis, 8—fenestra rotunda, 9—foramen centrale, 10—foramen singulare, 11—fossa for head of the malleus, 12—fossa incudis, 13—internal acoustic meatus, 14—posterior articular facet for tympanic bulla, 15—posterior process, 16—tractus spiralis foraminosus.

medial margins of dorsal premaxillary surfaces on proximal part of rostrum between antorbital notches flat instead of inclined medially toward mesorostral gutter, palatine bone and pterygoid sinus fossa extended farther anteriorly onto palate instead of ending at level of antorbital processes, post-orbital lobe of pterygoid sinus of middle ear air sinus system occupying large fossa on ventral surface of supraorbital process of frontal, internal acoustic meatus of periotic more elliptical and less circular in shape.

HOLOTYPE. CAS 4349, right periotic, collected by Charles Morrice in 1924.

TYPE LOCALITY. CAS locality 905, Sharktooth Hill Bonebed, Kern County, California.

PARATYPE. CAS 4347, left periotic collected by Charles Morrice in 1924 from CAS locality 905.

REFERRED SPECIMENS FROM THE SHARK-TOOTH HILL BONEBED. LACM 21256, an incomplete

skull lacking the extremity of the rostrum, the occipital shield, and the basicranium, from LACM locality 1625, and 31 isolated periotics as follows: CAS 4348, left (holotype of *Grypolithax pavidus*), CAS 4350, left (paratype of *G. pavidus*), both from CAS locality 905; LACM 21134, right, LACM 44916, left, LACM 63800, left, all from LACM locality 1625; LACM 21238, right, and LACM 48925, left, both from LACM locality 1557; LACM 39696, left, from LACM locality 3232; LACM 41473, left, from LACM locality 1655; LACM 58893, left, from LACM locality 6688; LACM 75371, left, from LACM locality 3208; LACM 96150, right, LACM 121998, LACM 121999, LACM 123477–123481, eight right, LACM 123482 and 123483 left, all from LACM locality 3162; LACM 98712, left, from LACM locality 3160; LACM 104094, left, from LACM locality 1622; LACM 123471–123473, three right, from LACM locality 4672; LACM 123474, left, from LACM locality 4874; LACM 123475, right, and LACM 123476, left, from LACM locality 4956.

FORMATION AND AGE. The holotype, paratype, and all specimens here referred to *Kentriodon obscurus* were collected from several localities scattered over several square kilometers in the Sharktooth Hill Bonebed in the upper part of the Round Mountain Silt. This bonebed is a single thin stratum and is the source of the Sharktooth Hill Local Fauna (Wood et al., 1941; Mitchell, 1966:28–29; Mitchell and Tedford, 1973; Barnes, 1976). It is correlated with the Barstovian North American land mammal age, the “Temblor” provisional provincial molluscan stage, the Relizian or Luisian foraminiferal stage, and is approximately between 13 and 15 million years old (Wood et al., 1941:31, pl. 1; Weaver et al., 1944:582, pl. 1; Evernden et al., 1964; Addicott, 1972; Savage and Barnes, 1972:133, 140; Berggren and Van Couvering, 1974: fig. 11; Barnes, 1976:326–327; 1978:5–6; Repenning and Tedford, 1977: table 1). Based on these correlations, the upper part of the Round Mountain Silt, including the bonebed, is approximately contemporaneous with the Calvert Formation in Virginia and Maryland (Gazin and Collins, 1950:3; Kellogg and Whitmore, 1957:1022; Ray, 1976: fig. 1).

DESCRIPTION AND COMPARISONS. Skull. The referred skull (LACM 21256, Figs. 2–7) of *Kentriodon obscurus* from the Sharktooth Hill Bonebed is incomplete and has suffered pre-depositional breakage and abrasion. The basicranium, occipital area, rostral extremity, vomer and pterygoid sinus fossae have been broken off. The sutures between the remaining bones were unfused, and the two halves were separated along the midline when the skull was found in the field. We have re-assembled it in its presumed original configuration based on comparisons with specimens of *Kentriodon pernix* from the Calvert Formation. Due to some distortion, however, the left supraorbital process fits incorrectly and attaches too low on the skull (Fig. 4a). On the right side (Fig. 4b) the supraorbital process is in the correct position. The measurements of the skull are as follows: total length as preserved, 193.5 mm; breadth of rostrum at antorbital notches, 67.7 mm; breadth of eranium at antorbital processes, 122.3 mm; interorbital width, 115.2 mm.

The skull is nearly the same size as both the holotype and

Kellogg's (1927a) referred skull of *K. pernix*. All three appear to represent young adult animals because none has the advanced suture fusion and/or extreme development of rugosities and processes seen on skulls of extremely old individuals of living delphinoids. Additionally, in the holotype skeleton of *K. pernix* most of the vertebral epiphyses, including those on cervicals and caudals, are tightly appressed to the vertebral centra but not fused, indicating that the individual had not yet achieved physical maturity. Overall skull shape and proportions are similar in the two species, as far as is known. It is in cranial details that the two species differ.

The open mesorostral gutter on the distal part of the rostrum is apparently characteristic of *Kentriodon pernix* (Kellogg, 1927a: pls. 2, 6), but is uncharacteristic of species in the family Kentriodontidae as a whole (Barnes, 1978: figs. 14–17). The premaxillae on the referred skull of *K. obscurus* are partly broken away distally, but in addition to having the usual wide open mesorostral gutter at the proximal end, they begin to diverge anteriorly as though they would have also left the gutter exposed distally as in *K. pernix*. There is no indication that the medial margins of the premaxillae were elevated adjacent to the posterior part of the mesorostral gutter as they are in *K. pernix*. The anterior (= rostral) parts of the premaxillae are comprised of bone which is denser and of smoother surface than the adjacent maxillae.

On the skull of *K. obscurus*, the premaxillary foramina are located on a transverse line between the antorbital notches (Figs. 2–3). These foramina are located more posteriorly on both the holotype and the referred skull of *K. pernix*. The premaxillary sulci associated with these foramina are somewhat damaged from breakage and abrasion, but between the right and left sides, the typical odontocete condition of three sulci (anteromedial, posteromedial, and posterolateral, see Barnes, 1978:13; Fordyce, 1981:1034, text-fig. 2) can be seen. Medial to the anteromedial sulcus and the premaxillary foramen, the premaxillary surface is rough and indicates the area where the nasal plug muscle was attached (Lawrence and Schevill, 1956: fig. 23; Mead, 1975). The part of the premaxilla that in life underlay the premaxillary sac (the premaxillary sac fossa of Fordyce, 1981:1035, text-fig. 2; Mead, 1975) lies posterior to the posteromedial and posterolateral sulci and lateral to the nares. This area is also roughened, but this is the result of postmortem abrasion because one small remnant of surficial bone on the left premaxilla indicates the previous existence of a thin, smooth bone surface on the premaxillary sac fossa as is typical of delphinoids. The more anterior location in *K. obscurus*, compared with *K. pernix*, of the premaxillary foramina, the three associated sulci, and concomitantly the anterior margin of the premaxillary sac fossae, is primitive, because these structures have moved progressively posteriorly during the odontocete cranial telescoping process (Miller, 1923). The area that was occupied by the premaxillary sacs is more elongate anteroposteriorly in *K. obscurus*, and we consider this to be primitive as well. These sacs in *Kentriodon* might have been symmetrical because the premaxillary sac fossae are not asymmetrical as they are in modern delphinids (cf. Mead, 1975).

Both species of *Kentriodon* have relatively small bony nares that are narrowly pointed anteriorly. This is also typical of many other species of Kentriodontidae (see Barnes, 1978: figs. 14–17), and contrasts with the large, round nares of species of Delphinidae.

The lateral margin of the maxilla dorsal to the posterior end of the tooth row and medial to the antorbital notch typically is formed into a relatively thick, horizontally projecting shelf in most kentriodontids. In *K. obscurus*, this part of the maxilla is proportionally wider and has a more squared off and vertical lateral margin than in *K. pernix*, in which the maxilla has a thinner, more rounded margin. The antorbital notches of *K. obscurus* are relatively narrower than those of *K. pernix*, because in *K. obscurus*, both the lacrimal and the maxilla project in a more anteromedial direction, thereby giving the antorbital process a different shape (Fig. 13).

On the supraorbital process, both the frontal and maxilla are significantly thicker and thus more convex or domed in *K. obscurus* than in *K. pernix*. The lateral margins of the maxillae have been both chipped and abraded over the orbit on the skull of *K. obscurus*. The frontal is therefore probably exposed more in dorsal view than it was in life.

The postorbital process of the frontal of *K. obscurus* is narrower, shorter, and more tapered distally than in *K. pernix*. These differences do not appear to be related to ontogeny because the juvenile skull that we refer to *K. pernix* (USNM 21027) from the Calvert Formation is smaller than the skull of *K. obscurus*, has characters indicating physical immaturity, but has substantially longer postorbital processes. Additionally, the postorbital processes on the three skulls of *Kentriodon pernix* from the Calvert Formation have a hook-like shape, in contrast to the straight process of *K. obscurus*.

Among modern Delphinidae, there is a fossa located at the posterolateral corner of the palate lateral to the pterygoid sinus fossa and which marks the position of an air sinus called the anterior sinus (see Fraser and Purves, 1960). This area of the palate of *K. obscurus* is convex and shows no development of such a fossa. On skulls of *K. pernix*, this area of the palate is distinctly less convex so that a transverse section through the proximal part of the rostrum is nearly V-shaped. Neither species has the type of fossa or concave area that in some living odontocetes marks the location of an anterior sinus, and there probably was no such sinus present in either species of *Kentriodon*.

The fossa for the lobe of the pterygoid air sinus that filled the pterygoid hamulus is larger and extends farther anteriorly in *K. obscurus* than in *K. pernix*. The roof of this pterygoid sinus fossa is marked by a tapered cavity on the ventral surface of the left palatine bone. The palatines concomitantly extend farther anteriorly and are more pointed in *K. obscurus*. The anterior-most extent of the palatines in *K. obscurus* is 35 mm anterior to the antorbital notch, whereas the same parameter on the holotype of *K. pernix* is only 10 mm and on Kellogg's referred skull (USNM 10670) it is 14.4 mm.

As on the referred skull (USNM 10670) of *K. pernix*, the ventral surface of the vomer was only exposed in a very narrow opening between the maxillae at about the middle of

the rostrum of *K. obscurus* (Figs. 14a, b). In both species, posterior palatine foramina flank this area, and slightly farther anteriorly a single anterior palatine foramen occurs in each maxilla adjacent to the posterior-most palatal exposure of the premaxillae.

The teeth of *K. obscurus* were significantly smaller in diameter than those of *K. pernix* (Figs. 14a, b). In *K. pernix*, throughout the tooth row, the alveoli have uniform diameter (3 mm) and nearly equal spacing. In *K. obscurus*, however, the alveoli that are still intact on the right side located just posterior to the mid-length of the rostrum are only 1.5 mm in diameter; one-half the size of those in *K. pernix*. The alveolar rows on both sides of the specimen of *K. obscurus* are incomplete because of breakage and abrasion. A row of eight consecutive alveoli in a distance of 32 mm in the right maxilla indicates that the species had more teeth than *K. pernix*, which Kellogg (1927a:32) estimated at about 40 on each side of each upper jaw. The alveoli of *K. obscurus* are oriented in the maxilla so that they face more laterally than in *K. pernix*. The alveolar rows do not extend as far posteriorly on the palate, and the posterior end of each tooth row curves medially toward the midline.

Posterior to the orbit, *K. obscurus* has a large, oval fossa in the ventral side of the supraorbital process of the frontal that measures approximately 15 by 20 mm. In modern delphinoids, a fossa in this location holds the postorbital lobe of the pterygoid air sinus (Fraser and Purves, 1960). We conclude that *K. obscurus* had a relatively large sinus here. On both the holotype and Kellogg's referred skull (USNM 10670) of *K. pernix*, there is only a slight depression at this place. This apparent difference in air sinus size is not clearly diagnostic because the juvenile referred skull, USNM 21027 of *K. pernix*, has a deep recess for the sinus at this place. Without a larger sample of specimens we cannot determine whether the size or the extent of invasion of bone by the sinus is variable in *K. pernix*, whether it is larger in geologically more recent individuals of *K. pernix* that occur higher in the Calvert Formation, or whether it is a significant taxonomic character that separates species.

Periotic. When Kellogg (1931) described *Grypolithax obscura* and *G. pavidia* from the Sharktooth Hill Bonebed, he noted only a few differences between their holotypes. He noted that the periotics of *G. pavidia* had a flatter cerebral surface. We now benefit from having a larger sample to study and find that, within the anticipated range of morphology of what we interpret as one species, the presence of a flat cerebral surface is variable.

Among the 31 isolated periotics from the Sharktooth Hill Bonebed that we refer to *Kentriodon obscurus*, there are at least six (LACM 63800, 48925, 21238, 41473, 75371, 123476) that are nearly identical in morphology to the periotic of the holotype of *K. pernix* (USNM 8060). Each of the others has some minor degree of difference. There was no periotic found with the skull we have referred to *K. obscurus*, and except for the holotype of *K. pernix*, there has been found only one other skull of *Kentriodon* sp. in the Calvert Formation that has an associated periotic. This specimen, USNM 187313, which we believe is a different and probably undescribed



Figure 2. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, dorsal view, natural size.

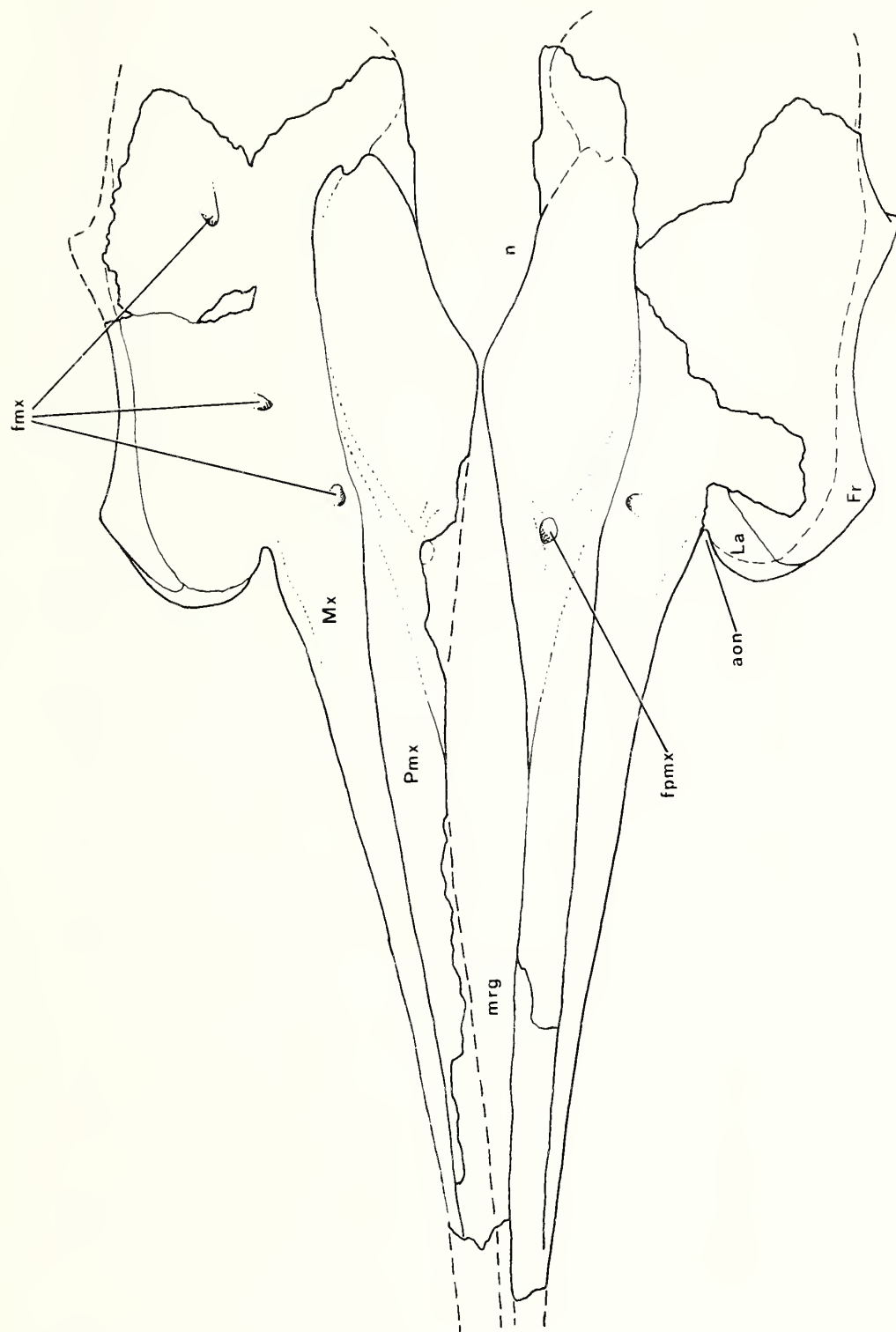


Figure 3. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, dorsal view, natural size. Abbreviations: aon—antorbital notch, fmx—maxillary foramen, fpmx—premaxillary foramen, fr—frontal, la—lacrimal, mrg—mesorostral gutter, mx—maxilla, n—narial opening, pmx—premaxilla.



Figure 4. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, a, left lateral view; b, right lateral view, natural size.

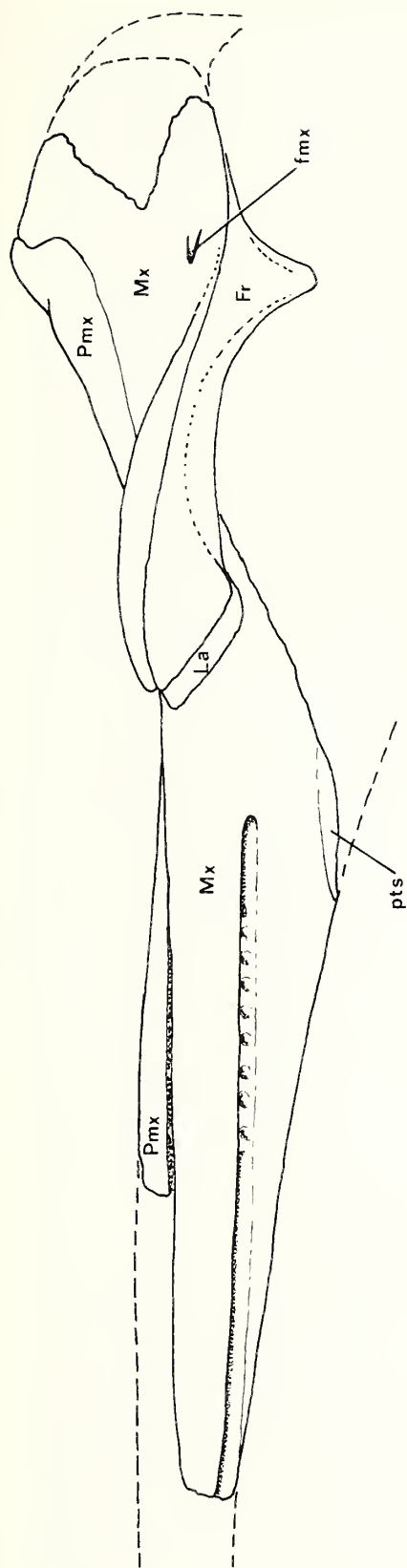


Figure 5. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, composite left lateral view based on both sides of skull, natural size. Abbreviations: fm x — maxillary foramen, Fr — frontal, La — lacrimal, Mx — maxilla, Pmx — premaxilla, pts — fossa for pterygoid sinus of the middle ear air sinus system.

Table 1. Some characters differentiating *Kentriodon pernix* and *K. obscurus*. An asterisk denotes the more derived character states, as deduced from the morphology of *Agorophius* and species of *Squalodontidae*.

<i>Kentriodon obscurus</i>	<i>Kentriodon pernix</i>
1. Premaxillary foramina between level of antorbital notches.	1. Foramina posterior to level of notches.*
2. Lateral maxillary margin anterior to antorbital notches thick and squared off.*	2. Lateral margin thin and rounded.
3. Antorbital notch narrow.	3. Antorbital notch wider.*
4. Premaxillae flat in area of attachment of nasal plug muscles.*	4. Premaxillae elevated medially.
5. Postorbital process of frontal short and thick.*	5. Process long and curved.
6. Alveoli for teeth small (circa 1.5 mm in diameter).	6. Alveoli larger (circa 3 mm in diameter).*
7. Posterior end of alveolar row bends medially on palate.	7. Posterior end of alveolar row follows lateral margin of palate.*
8. Teeth implanted in middle and posterior part of alveolar row so as to face ventrolaterally.*	8. Teeth face more ventrally.
9. Palatines and pterygoid air sinus fossae on palate extend farther anteriorly beyond location of antorbital processes.*	9. Palatines and fossae do not extend beyond level of antorbital processes.
10. Posterior part of palate lateral to fossae for pterygoid air sinus convex.	10. Palatal surface less convex.*
11. Large fossa in ventral surface of frontal for postorbital lobe of pterygoid air sinus.*	11. Fossa small or absent.
12. Internal acoustic meatus of periotic elliptical in shape.	12. Meatus circular in shape.*

species of *Kentriodon* was collected from Zone 14, near the top of the Calvert Formation, and the skull, periotic, and postcranial skeleton show several significant differences from the holotype and referred specimen of *K. pernix*. The periotic of this specimen, USNM 187313 (Figs. 8a, 9a), has a prominent, elevated, flat area on its cerebral surface that is more pronounced than on any of the other periotics referred to



Figure 6. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM 1625, ventral view, natural size.

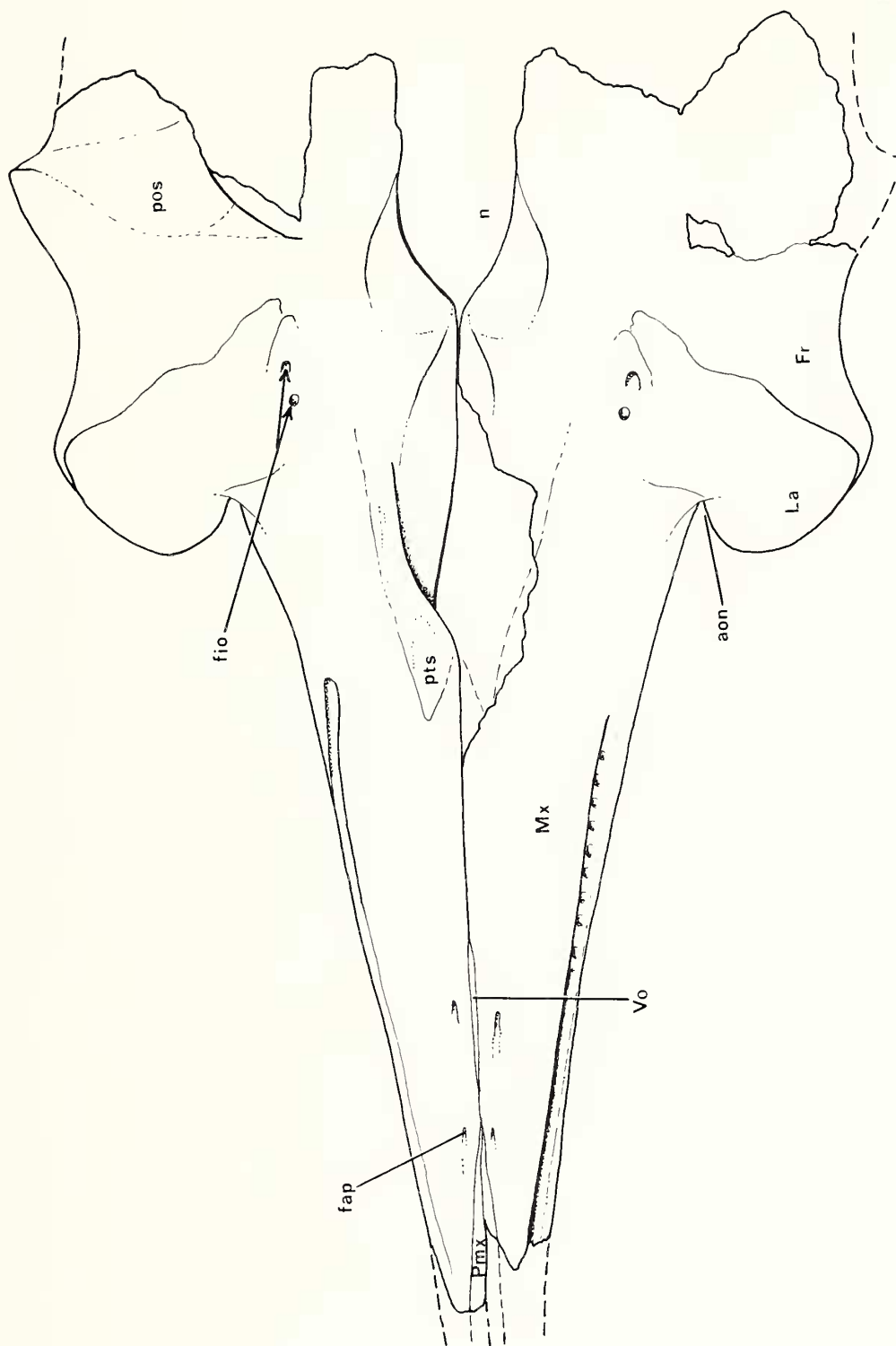


Figure 7. *Kentriodon obscurus* (Kellogg, 1931), referred skull, LACM 21256 from LACM locality 1625, ventral view, natural size. Abbreviations: aon—anteorbital notch, fap— anterior palatine foramen, fio—orbital apertures of the infraorbital foramen, Fr—frontal, La—lacrimal, Mx—maxilla, n—nasal opening, pos—fossa for postorbital lobe of the pterygoid sinus of the middle ear air sinus system, Pmx—premaxilla, pts—fossa for pterygoid sinus of the middle ear air sinus system, Vo—cleft that originally contained the palatal exposure of the vomer.

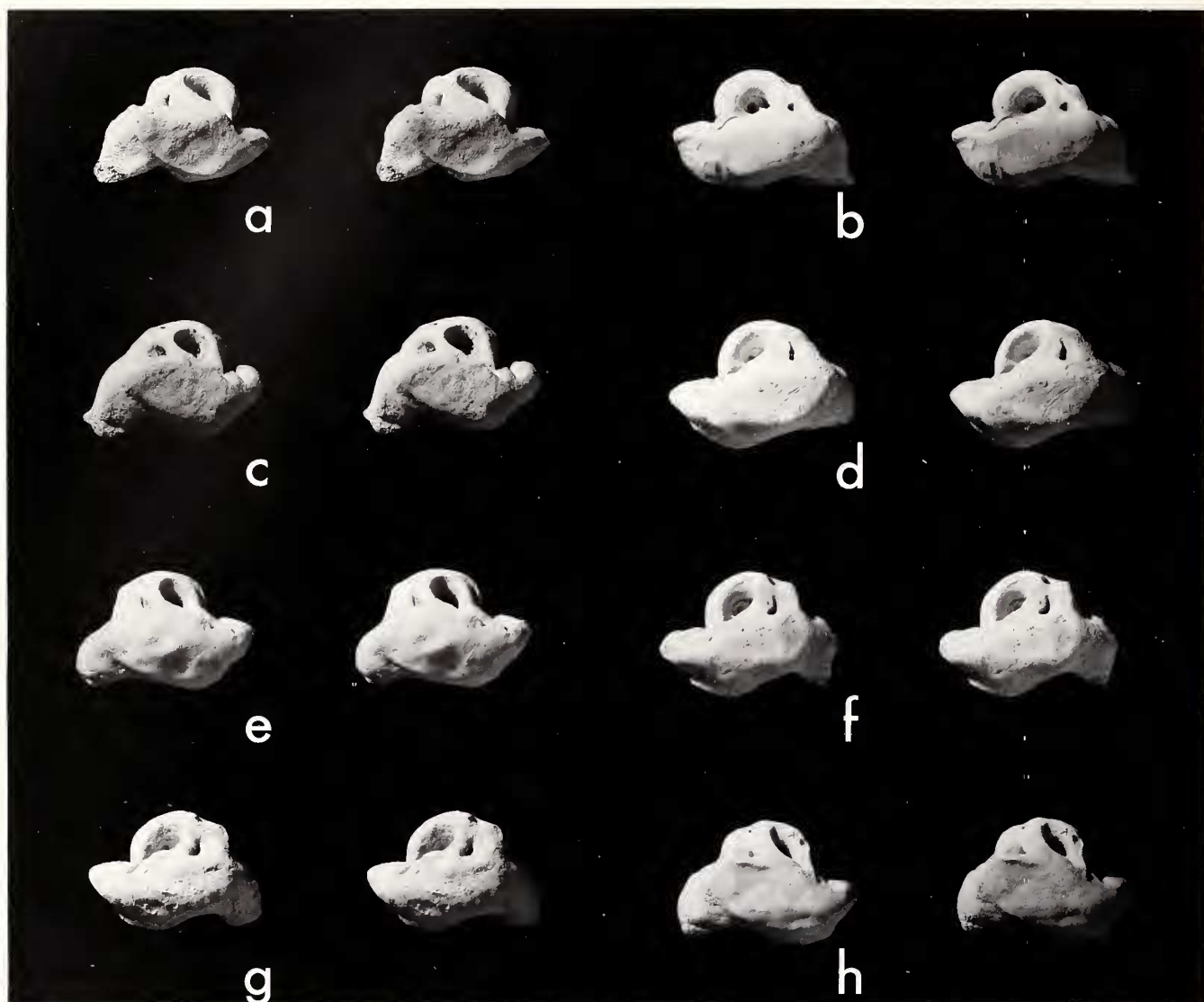
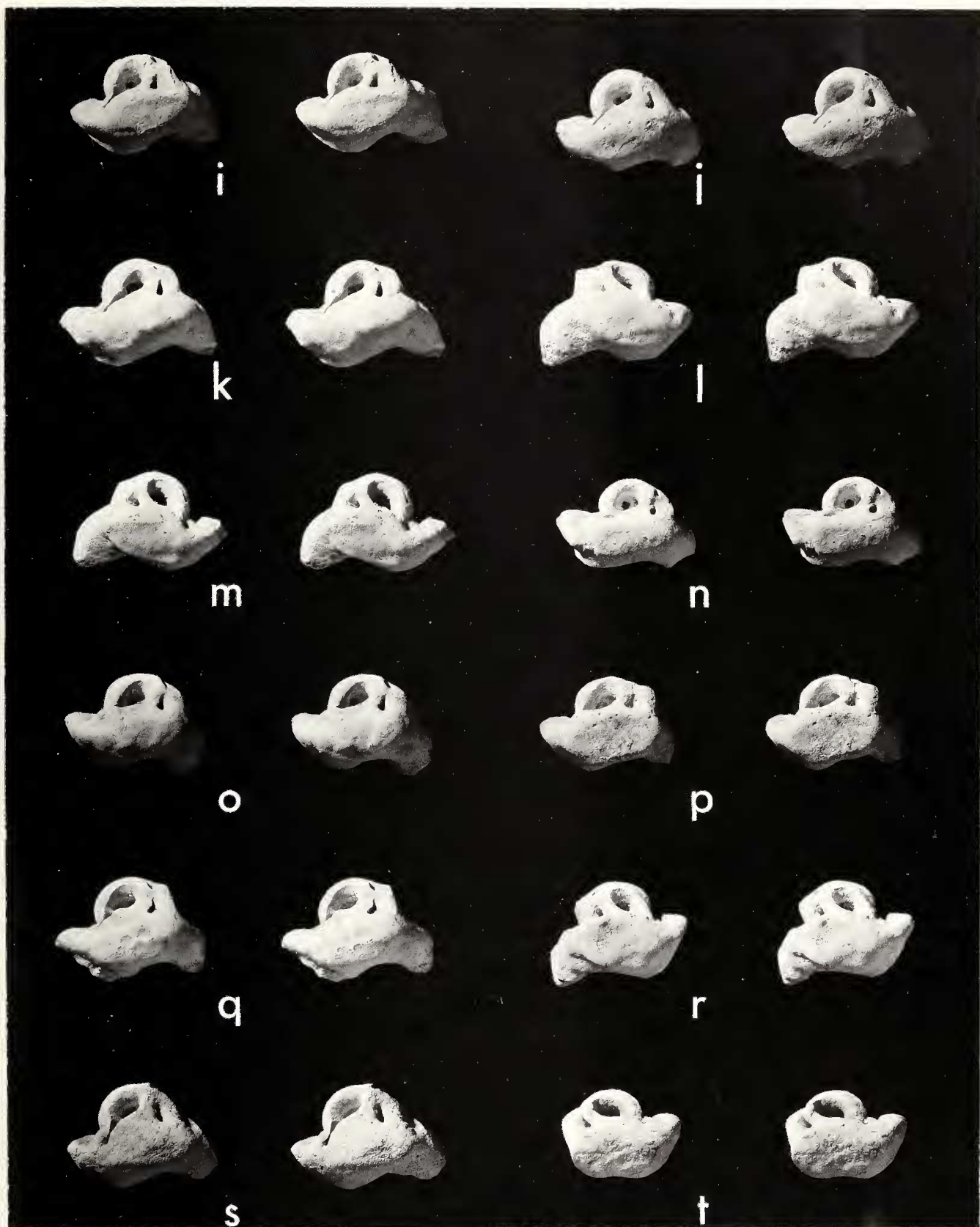


Figure 8. Periotics of *Kentriodon* Kellogg, 1927: a, *Kentriodon* sp., Calvert Fm., Virginia, USNM 187313, right; b, *Kentriodon pernix* Kellogg, 1927, holotype, USNM 8060, left; c, *Kentriodon* sp., Calvert Fm., Virginia, USNM 214754, right; *Kentriodon obscurus* (Kellogg, 1931) from the Sharktooth Hill Bonebed; d, LACM 41473, left; e, CAS 4349, holotype, right; f, CAS 4348, left (holotype of *Grypolithax pavida* Kellogg, 1931); g, CAS 4350, left (paratype of *Grypolithax pavida*); h, LACM 75371, right; i, LACM 63800, left; j, LACM 48925, left; k, CAS 4347, paratype, left; l, LACM 21238, right; m, LACM 121998, right; n, LACM 58893, left; o, LACM 104094, left; p, LACM 44916, left; q, LACM 98712, left; r, LACM 21134, right; s, LACM 39696, left; t, LACM 96150, right; all figures are stereophotographs of the cerebral (or dorsal) surface, natural size.

Kentriodon. Such a flat surface is present, however, in varying lesser degrees on eight of the periotics from the Sharktooth Hill Bonebed referred to *K. obscurus* (including the holotype of *Grypolithax pavida*), as well as on the holotype periotic of *K. pernix*. Another isolated periotic (USNM 214754, Figs. 8c, 9c) from the Calvert Formation in Virginia closely matches the holotype periotic of *K. pernix*, and although it has a more rounded cerebral surface, we refer it to that species.

All of the periotics from the Sharktooth Hill Bonebed that we refer to *Kentriodon obscurus* resemble the holotype peri-

otic of *K. pernix* by having the following characters: (1) similar size; (2) relatively small anterior and posterior processes; (3) an overall sinuosity in either cerebral or ventral view owing to the fact that the anterior process is bent medially and the posterior process is bent laterally; (4) cochlear portion relatively small and broadly joined to the body of the periotic, not narrowly joined to the body and extended medially as in many primitive odontocetes; (5) posterior process bent ventrally at a sharp angle from the body of the periotic thereby forming a sharp peak or angle on the posterior part of the



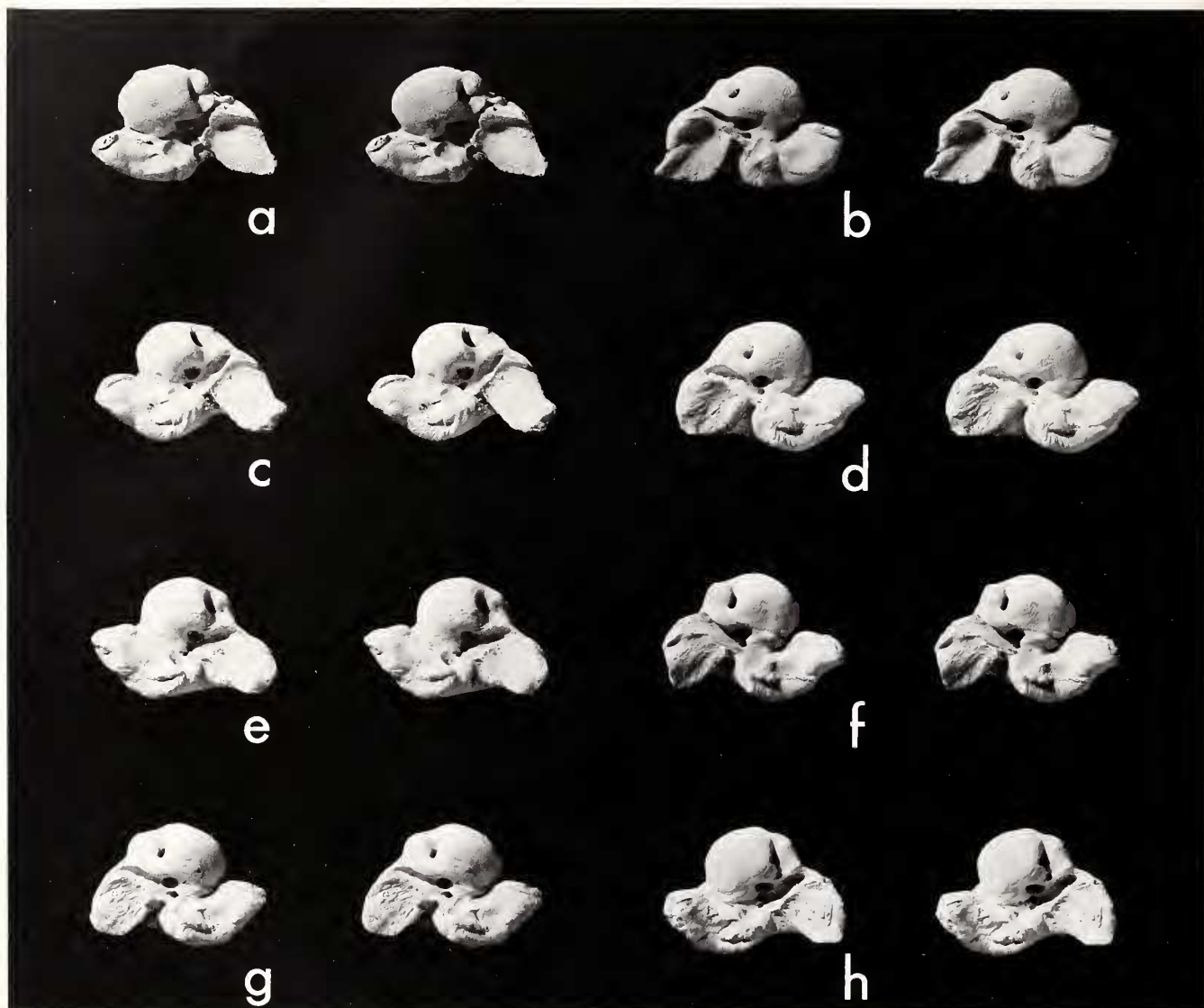


Figure 9. Periotics of *Kentriodon* Kellogg, 1927: **a**, *Kentriodon* sp., Calvert Fm., Virginia, USNM 187313, right; **b**, *Kentriodon pernix* Kellogg, 1927, holotype, USNM 8060, left; **c**, *Kentriodon* sp., Calvert Fm., Virginia, USNM 214754, right; *Kentriodon obscurus* (Kellogg, 1931) from the Sharktooth Hill Bonebed; **d**, LACM 41473, left; **e**, CAS 4349, holotype, right; **f**, CAS 4348, left (holotype of *Grypolithax pavida* Kellogg, 1931); **g**, CAS 4350, left (paratype of *Grypolithax pavida*); **h**, LACM 75371, right; **i**, LACM 63800, left; **j**, LACM 48925, left; **k**, CAS 4347, paratype, left; **l**, LACM 21238, right; **m**, LACM 121998, right; **n**, LACM 58893, left; **o**, LACM 104094, left; **p**, LACM 44916, left; **q**, LACM 98712, left; **r**, LACM 21134, right; **s**, LACM 39696, left; **t**, LACM 96150, right; all figures are stereophotographs of the tympanic (or ventral) surface, natural size.

cerebral surface; (6) anterior process bent anteroventrally and having a groove or pit on its medial side; (7) the cleft between the anterior process and the cochlear portion bearing a small crease between the groove for the tensor tympani muscle and the cochlear portion; (8) articular facet for the auditory bulla on the posterior process large, concave and striated; and (9) a raised rugosity lateral to the fossa for the head of the malleus.

Statistical analysis of the Sharktooth Hill Bonebed sample

of *K. obscurus* periotics (Table 2) proved useful. The parameters chosen were width and length measurements. The measurement of the cochlear portion is probably less variable individually or allometrically than the other two, because the sizes of the anterior and posterior processes apparently change during ontogeny. Measurements of the holotype of *K. obscurus* fall within the range of measurements for the sample, and they differ from the mean less than the standard deviation in all three parameters. The same situation exists when

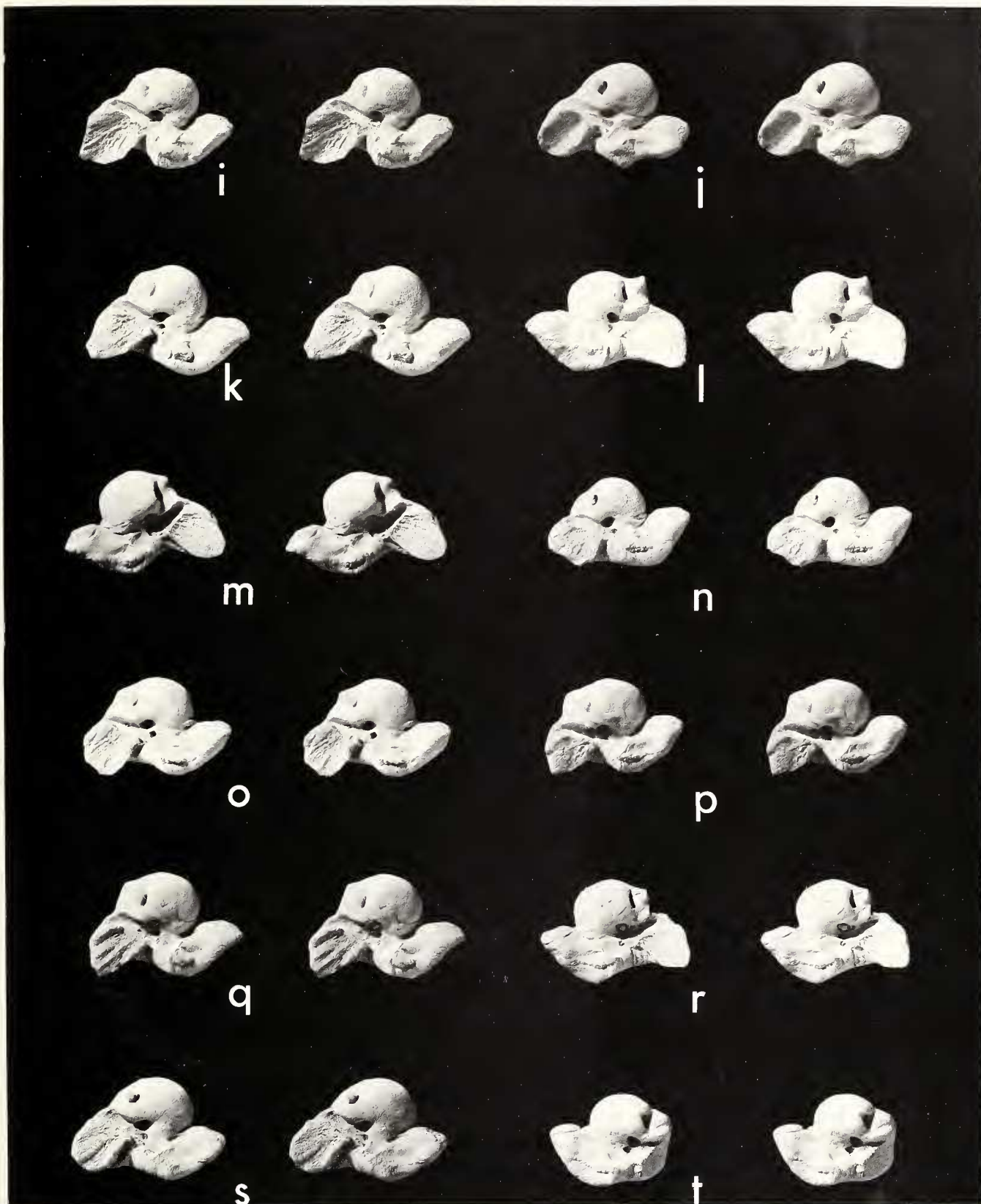


Table 2. Statistical comparisons of the holotype periotic of *Kentriodon pernix* and the holotype and referred periotics of *K. obscurus* from the Sharktooth Hill Bonebed.

Measurement	Number	Bonebed sample of <i>K. obscurus</i> *				<i>K. obscurus</i> holotype		<i>K. pernix</i> holotype	
		Observed range	Mean	Standard deviation	Coefficient of variation	Measurement	Difference from mean	Measurement	Difference from mean
Total length	27	25.2–29.4	27.2	1.2	4.41	26.9	–0.3	28.3	1.1
Width at pars cochlearis	29	16.5–19.5	18.0	0.8	4.44	18.2	0.2	17.4	–0.6
Antero-posterior dimension of pars cochlearis	28	13.2–15.9	14.7	0.7	4.76	14.1	–0.6	14.2	–0.5

* Sample includes paratype of *K. obscurus* and holotype and paratype of *Grypolithax pavidus*.

the holotype of *K. pernix* is compared to the sample of *K. obscurus*, except that it differs somewhat more from the mean than does the holotype of *K. obscurus*, but is still within the standard deviation.

The similarities among these periotics from the Atlantic and Pacific coasts are not surprising. Kasuya (1973:72) and Barnes (1976:321–322, 327) have pointed out that periotics of congeneric species of cetaceans are very similar and that in some instances closely related modern or fossil species simply may not be differentiated based on periotics alone.

Among the periotics of *K. obscurus*, some characters are variable. These are: (1) shape and relative size of the posterior articular facet for the bulla; (2) degree of rugosity of this articular facet; (3) position of the groove or pit on the medial side of the anterior process; (4) presence or absence of a tuberosity on the posterior side of the cochlear portion between the *fenestra rotunda* and the orifice of the *aquaeductus cochleae*; (5) extent of development of an attenuated groove in the anterior margin of the internal acoustic meatus at the cerebral orifice of *aquaeductus Fallopii*; and (6) extent of development of a flat area on the cerebral surface of the body of the periotic in contrast with a rounded, convex surface. The only character that we recognize whereby the holotype periotic of *Kentriodon pernix* may be separated from this sample of periotics of *K. obscurus* is its more circular internal acoustic meatus. Every other character exists in at least one of the periotics from the Sharktooth Hill Bonebed that we refer to *K. obscurus*.

The only other significantly large, documented sample of periotics of a species of Kentriodontidae is the series of *Liolithax kernensis* from the Sharktooth Hill Bonebed that was described and analyzed by Barnes (1978). The periotics from the bonebed that we now refer to *Kentriodon obscurus* are as variable as the sample Barnes referred to *L. kernensis*. These periotics are not referable to any of the other odontocetes that Kellogg (1931) named based upon periotics from the Sharktooth Hill Bonebed.

Among these other species, the problematic odontocete *Platylithax robusta* Kellogg, 1931, the primitive sperm whale *Aulophyseter morricei* Kellogg, 1927, the platanistoid dolphin “*Squalodon*” *errabundus* Kellogg, 1931, and the ken-

triodontid dolphin *Liolithax kernensis* all have periotics that are substantially different from those belonging to *Kentriodon*. Periotics of another dolphin, *Loxolithax sinuosa* Kellogg, 1931, differ subtly by being flatter dorsoventrally, having a larger cochlear portion, a differently shaped posterior process, a larger fossa for the head of the malleus, a groove on the lateral surface of the anterior process, and by lacking any notable flattening of the cerebral surface. Periotics of the two species of *Lamprolithax* Kellogg, 1931, differ from those of *Kentriodon* in many of the same ways as do those of *Loxolithax sinuosa*. *Nannolithax gracilis* Kellogg, 1931, has a smaller periotic with a large anterior process. *Oedolithax mira* Kellogg, 1931, has a larger periotic with a deeper cleft separating the anterior process from the cochlear portion.

cf. *Kentriodon* sp.

Figures 10–11

cf. *Kentriodon* Kellogg, 1927. Barnes, 1976:326.

REFERRED SPECIMENS. LACM 29549, left periotic, collected by Richard W. Huddleston in 1969 from LACM locality 3066, Kern River, Kern County, California; and UCMP 83605, right periotic, collected by Richard C. Bishop from UCMP locality V-6953, Kern County, California.

FORMATION AND AGE. Both of these specimens are from localities stratigraphically below the Sharktooth Hill Bonebed in the lower part of the Round Mountain Silt. This part of the formation is early Middle Miocene in age, about 15 to 19 million years old (see Barnes, 1976:326). Savage and Barnes (1972:133) have reported Hemingfordian land mammals from these same strata. Addicott (1972) characterized the age of these beds further as representing part of the “Temblor” provisional provincial molluscan stage and the upper part of the Saucian or the Relizian foraminiferal stage.

DESCRIPTION AND COMPARISONS. These two periotics differ from each other in both size and morphology and may actually represent two different species. Each shares characters in common with both *Kentriodon obscurus* and *K. pernix*, such as the strong apex on the cerebral surface

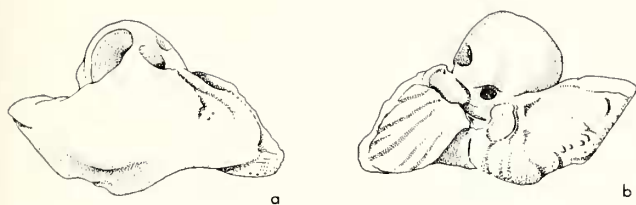


Figure 10. cf. *Kentriodon* sp., left periotic, LACM 29549 from LACM locality 3066; **a**, cerebral or dorsal view; **b**, tympanic or ventral view; both natural size.

posterolateral to the orifice of *aquaeductus vestibuli*, small internal acoustic meatus, and anteromedially projecting anterior process—all characters that could be regarded as primitive. The smaller of the two periotics, UCMP 83605, has an anteroposteriorly elongate cochlear portion as in other specimens of *Kentriodon*. The larger periotic, LACM 29549, has a relatively smaller and more globose cochlear portion, and in this respect it resembles the holotype periotic of the primitive kentriodontid *Kampholophos serrulus* Rensberger, 1969 (see Rensberger, 1969: pl. 4, figs. f–h).

aff. *Delphinodon dividum* True, 1912

Figure 12

cf. *Delphinodon dividum* True, 1912. Barnes, 1976:326.

REFERRED SPECIMEN. LACM 41041, left periotic with stapes, lacking extremity of posterior process, collected by the late John E. Fitch, about 1970 from LACM locality 6602, "Barker's Ranch Faunal Site," Kern County, California.

FORMATION AND AGE. This specimen is from a locality in the lower part of the Round Mountain Silt, below the Sharktooth Hill Bonebed, in roughly the same strata as the two previously described periotics. Its age is likewise early Middle Miocene and between approximately 15 and 19 million years old.

DESCRIPTION AND COMPARISONS. The comparisons that we have made are specifically only with *Delphinodon dividum*, because that is the only species of the genus for which a periotic is known. The holotype is a specimen collected from the Calvert Formation and includes a skull, mandible, and part of the postcranial skeleton. The type species of the genus, *D. mento* Cope, 1868, as fixed by Hay (1902), is known only by teeth.

As noted by Barnes (1976:326) this periotic closely resembles that of *Delphinodon dividum*. *Kentriodon* spp. and *Delphinodon dividum* are closely related (cf. Kellogg, 1927a, 1928: 67–69; Slijper, 1936:556), and both have been classified in the subfamily Kentriodontinae (Barnes, 1978). The periotic with the holotype of *Delphinodon dividum* (see True, 1912: pl. 25, figs. 6, 7) has many characters in common with the isolated periotic (LACM 41041) from Kern County. Notable among these are the large fossa for the head of the malleus, the globose anterior process which is bent medially, and the small, spherical cochlear portion. The periotic of *D. dividum* is somewhat similar in overall shape to periotics of *Kentriodon obscurus* and *K. pernix*, but differs by not having the

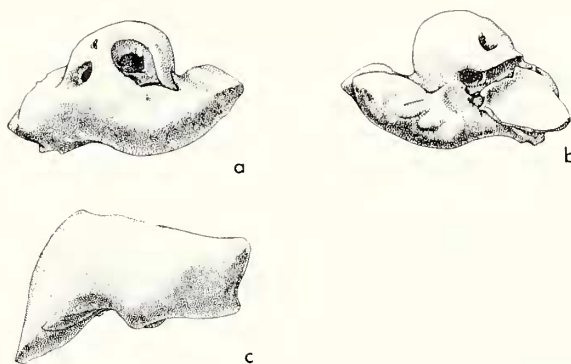


Figure 11. cf. *Kentriodon* sp., right periotic, UCMP 83605 from UCMP locality V-6953; **a**, cerebral or dorsal view; **b**, tympanic or ventral view; **c**, lateral view; all natural size.

cochlear portion as broad anteroposteriorly, by having the anterior process bent more medially, and by having the cochlear portion separated from the anterior process by a much deeper fissure. The isolated periotic from Kern County (LACM 41041) differs from the holotype of *D. dividum* by being smaller, having a relatively smaller posterior articular facet for the bulla, and by having a relatively smaller and narrower internal acoustic meatus. The latter character may be primitive in comparison with *D. dividum*. We believe this isolated periotic from the Round Mountain Silt is congeneric with *Delphinodon dividum* and represents an earlier, more primitive species.

A very closely related, if not identical, species is represented by a periotic from correlative rocks in Japan. Okazaki (1976:37–38, text-fig. 6, pl. 11, figs. 1a–c (where the scale is incorrect)) has identified that periotic, collected from the late Early or early Middle Miocene Natak Formation, as a rhabdosteoid dolphin, *Eurhinodelphis* sp. B. We do not concur with that generic allocation because the periotic described by Okazaki does not closely resemble periotics found in skulls of *Eurhinodelphis* spp. collected from the Calvert Formation in Maryland and Virginia (USNM collections). Instead, we believe the periotic from Japan very closely resembles the periotic of *Delphinodon dividum*, and the one from California that we identify here as aff. *Delphinodon dividum*, although it apparently is considerably larger than the latter. We conclude that the specimen from the Natak Formation should

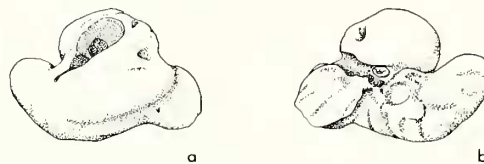


Figure 12. aff. *Delphinodon dividum* True, 1912, left periotic, LACM 41041 from LACM locality 6602; **a**, cerebral or dorsal view; **b**, tympanic or ventral view; both natural size.

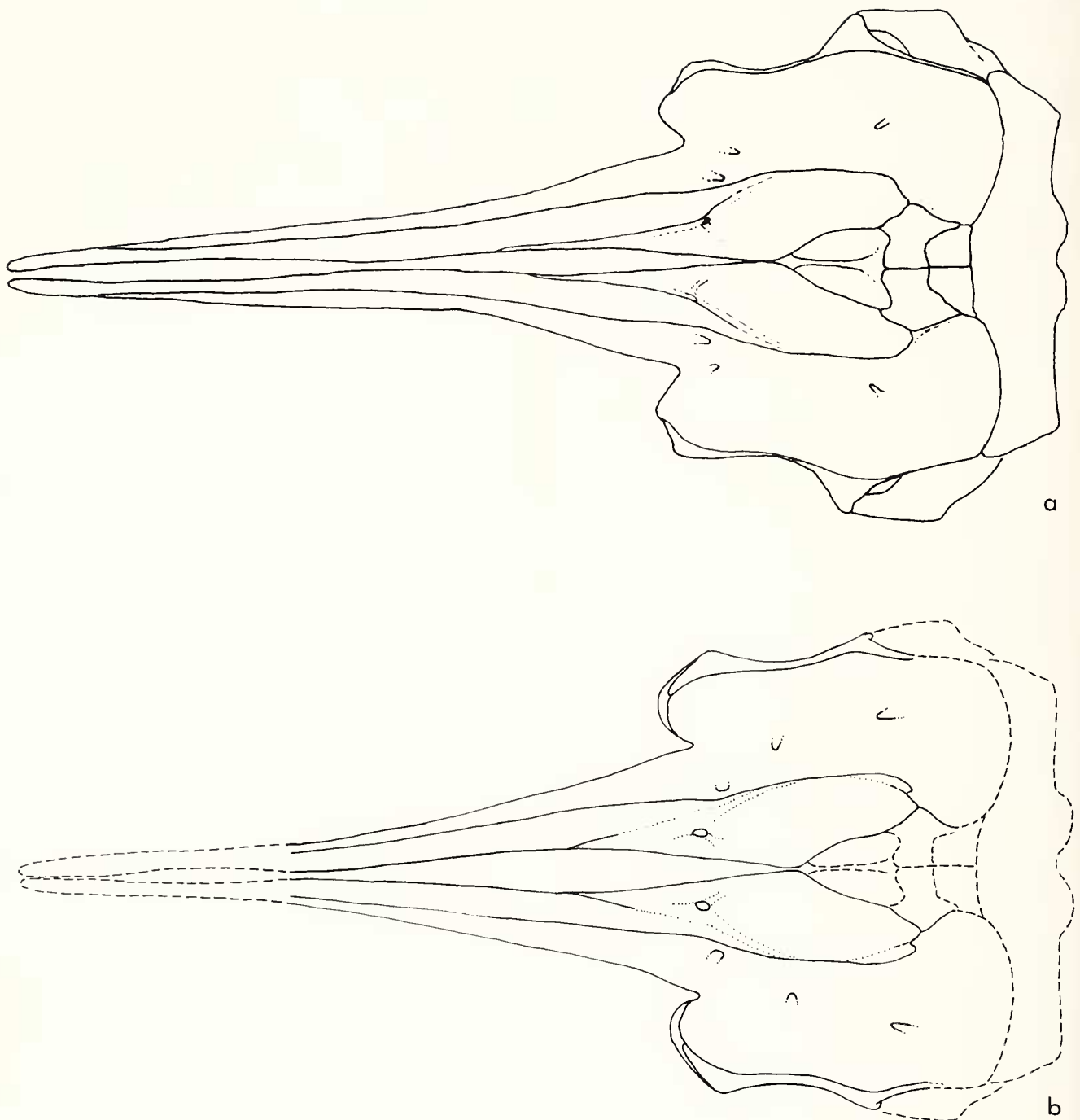


Figure 13. Reconstructions of dorsal views of skulls of *Kentriodon* Kellogg, 1927; **a**, *Kentriodon pernix* Kellogg, 1927, based on the holotype, USNM 8060, and the referred specimen, USNM 10670; **b**, *Kentriodon obscurus* (Kellogg, 1931), based on the referred specimen, LACM 21256, with outline of the rostral extremity and brain case from *K. pernix*; both at different scales, but reduced to the same brain case length (antorbital notches to condyles). (a from Kellogg, 1927: pls. 2, 6, and Barnes, 1978: fig. 14, c; b from our Fig. 2.)

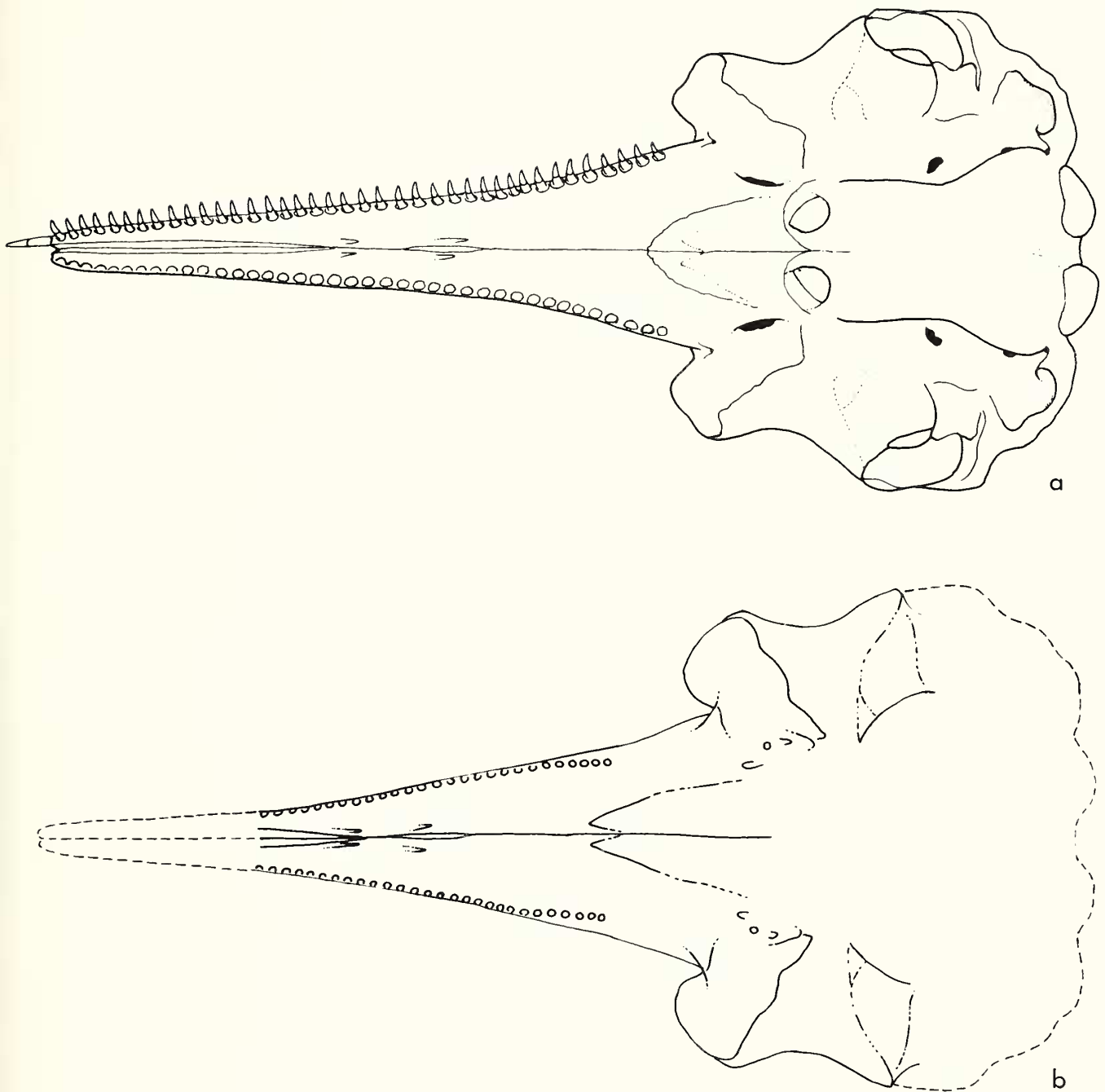


Figure 14. Reconstructions of ventral views of skulls of *Kentriodon* Kellogg, 1927; **a**, *Kentriodon pernix* Kellogg, 1927, based on the holotype, USNM 8060, and the referred specimen, USNM 10670, with the dentition omitted on one side so that the size and number of alveoli may be seen; **b**, *Kentriodon obscurus* (Kellogg, 1931), based on the referred specimen LACM 21256, with outline of the rostral extremity and brain case from *K. pernix*; both at different scales, but reduced to the same brain case length. (**a** from Kellogg, 1927: pls. 4, 5, 7 and 8; **b** from our Fig. 6.)

be re-identified as Kentriodontinae, aff. *Delphinodon dividum*.

DISCUSSION

RELATIVE ABUNDANCE OF *KENTRIODON OBSCURUS* IN THE SHARKTOOTH HILL BONEBED

A list of 15 odontocetes in the Sharktooth Hill Bonebed given by Barnes (1976:327, table 3) included 11 named species and four possibly undescribed species. *Grypolithax pavidus* may now be deleted from that list because it is a synonym of *K. obscurus*. Each of the 14 remaining species is recognized by periotics. Some of the species in polytypic genera that are known only by periotics may be questionably valid (Barnes, 1976:327). The abundant sperm whale, *Aulophyseter morricei*, with quite distinctive periotics, is known by other skeletal elements. The platanistoid "*Squalodon*" *errabundus* also has distinctive periotics and is known from other skeletal elements, however, it is relatively rare in the bonebed, and we (unpublished data) have been able to collect or locate only 31 of the highly unique periotics of that species. Similarly, the distinctive periotics of the kentriodontid *Liolithax kernensis* total only 42 in number (Barnes, 1978). Only *Platylithax robusta*, known solely by the holotype, and the other four unidentified odontocete species are rarer in samples than *Kentriodon obscurus*. The total sample of *K. obscurus* amounts to only one skull and 31 periotics, and on this evidence the species ranks as one of the rarest odontocetes in the Sharktooth Hill Bonebed. The remaining hundreds of periotics in museum collections can be identified as belonging to species of the genera *Loxolithax* Kellogg, 1931, *Oedolithax* Kellogg, 1931, *Lamprolithax*, or *Nannolithax* Kellogg, 1931.

ZOOGEOGRAPHY

Fossil Kentriodontidae have been reported from the North Atlantic, the South and North Pacific, and the Paratethys regions. All the species included by Barnes (1978:26) in this family were Middle or Late Miocene in age. Fordyce (1980:328) has subsequently reported a kentriodontid from Late Oligocene rocks of New Zealand. The fossils from early Middle Miocene rocks in California identified as cf. *Kentriodon* sp. and aff. *Delphinodon dividum* in this paper constitute the earliest records for the family in the North Pacific region. These, along with the sample we regard as *Kentriodon obscurus* from the Sharktooth Hill Bonebed, the kentriodontids from Japan, and Late Miocene species from California (Barnes, 1976) suggest that a considerable diversity of species in this family inhabited the North Pacific Ocean during the Miocene. This diversity equals that known for kentriodontids during the Middle and Late Miocene in the North Atlantic and Paratethys regions (see Barnes, 1978:26). The family might have been cosmopolitan during the Miocene, but there are as yet no kentriodontids recognized from the South Atlantic realm or from the eastern South Pacific. It would be premature to speculate on the place of origin of the family,

even though the oldest known occurrence is in the South Pacific.

Barnes (1976:338) noted that the then available paleontologic literature suggested a pattern of generic cosmopolitanism among larger fossil late Tertiary cetaceans and one of generic endemism within major northern ocean basins among the smaller fossil odontocetes. Among the nine currently recognized genera of Kentriodontidae (cf. Barnes, 1978:26), more than one-half (i.e. *Liolithax* Kellogg, 1931, *Kentriodon*, *Delphinodon* Leidy, 1869, *Pithanodelphis* Abel, 1905, and *Lophocetus* Cope, 1868) are now known by species in both the North Atlantic and the North Pacific regions. For the Kentriodontidae, it now appears that within ocean basins a pattern of endemism at the species level rather than the generic level prevailed.

PHYLOGENETIC RELATIONSHIPS

Kentriodon is the most primitive genus yet assigned to the subfamily Kentriodontidae. For example, *Kentriodon* lacks such derived characters as the elevated cranial vertex and enlarged nasal bones of *Pithanodelphis*, and the short rostrum, bulbous braincase and rounded facial margins of *Delphinodon dividum*. The cranial morphology of *Kentriodon* suggests that its origin might have been among more primitive species in the subfamily Kampholophinae. *Kentriodon* shares with the kampholophine species *Liolithax pappus* and *Kampholophos serrulus* such primitive characters as a narrow, elongate rostrum, high tooth count, low cranial vertex, and a concave margin of the facial region above the orbit. *Kentriodon* is more derived, however, than either of those species, by having facial surfaces of the frontal and the maxilla that are spread more over the dorsal opening of the temporal fossa. The extent of this spreading, however, had not progressed to the stage seen in the derived kentriodontine genera *Delphinodon*, *Leptodelphis* Kirpichnikov, 1954, *Microphocaena* Kudrin and Tatarinov, 1965, *Pithanodelphis* and *Sarmatodelphis* Kirpichnikov, 1954.

There are possibly relationships between Kentriodontinae and primitive modern Delphinidae, such as species in the subfamily Steninae (*sensu* Mead, 1975), and this has been discussed previously by True (1912), Kellogg (1927), and Barnes (1978). Similarities exist in overall cranial proportions, shape of the mandible, and size and numbers of teeth, but kentriodontines are more primitive by having symmetrical cranial vertices, less extensive air sinuses and unfused cervical vertebrae.

The two essentially synchronous species, *Kentriodon pernix* and *K. obscurus*, have different combinations of both primitive and derived characters (see Table 1). For example, *K. pernix* is more derived than *K. obscurus* by having the premaxillary foramina located more posteriorly (Fig. 13), and the posterior part of the palate less convex on either side of the pterygoid sinuses. *Kentriodon obscurus*, on the other hand, is more derived by having shorter postorbital processes of the frontals, smaller teeth (Fig. 14), medial premaxillary sur-

face in front of the nares not inclined, a longer anterior extension of the palatine bones on the palatal surface and of the pterygoid air sinuses within the pterygoid hamuli, and a larger postorbital lobe of the pterygoid air sinus. The derived character states listed in Table 1 are equally spread between the two species. The polarity of these characters was determined by comparisons with species in the more primitive odontocete families, Squalodontidae and Agorophiidae.

Kentriodon pernix and *K. obscurus* might have evolved from a common ancestor, and the discoveries of the older fossils of kentriodontines in California certainly indicate that such *Kentriodon*-like dolphins lived prior to Middle Miocene time in the North Pacific Ocean.

CONCLUSIONS

A fossil delphinoid genus, *Kentriodon* Kellogg, 1927, that is uncommon in northwest Atlantic Middle Miocene rocks, occurs in contemporaneous rocks on the eastern margin of the North Pacific Ocean. A few fossils from the North Pacific margin identified as this genus or related genera of small dolphins have been briefly cited in previous literature, and it is shown here that the genus *Grypolithax* Kellogg, 1931, originally based on specimens from the Middle Miocene Sharktooth Hill Bonebed in California, is synonymous with *Kentriodon*. Based on isolated fossil periotics, Kellogg (1931) had named two species in *Grypolithax*, *G. obscura* Kellogg, 1931, and *G. pavid*a Kellogg, 1931. These are the only species that have ever been assigned to *Grypolithax* and we regard them as synonymous. *G. obscura* has page priority, is the senior synonym of *G. pavid*a, and is the type species of the genus. Because *Grypolithax* is not valid, the most appropriate binomen for the species from the Sharktooth Hill Bonebed is *Kentriodon obscurus* (Kellogg, 1931). We refer periotics and a partial skull to this species. The only other named species of *Kentriodon* is the type species, *K. pernix* Kellogg, 1927, from the Calvert Formation in Maryland.

Among possibly as many as 14 species of odontocetes found in the Sharktooth Hill Bonebed, *K. obscurus* is not abundant and is one of the rarest species. Only one of the rarer ones, *Platylithax robusta* Kellogg, 1931, has been named previously in the scientific literature. The other four have not been named, although Barnes (1976) has called attention to their presence. Only by increasing the total sample size will we be able to eventually recognize the rarer species in the Sharktooth Hill Local Fauna and learn their anatomy.

Middle Miocene fossils of *Kentriodon* have now been reported from Maryland and California in the U.S.A., and apparently also from Japan. The earliest reported kentriodontine fossils from the eastern North Pacific region are two isolated periotics we have identified as cf. *Kentriodon* sp. from the early Middle Miocene part of the Round Mountain Silt, lower stratigraphically than the Sharktooth Hill Bonebed. *Kentriodon* may have been a cosmopolitan genus in the Middle Miocene, but there is yet no published fossil evidence from the southern hemisphere to prove this.

Each of the two known species of *Kentriodon* has a different

suite of primitive and derived characters, and the two are probably derived from a common ancestor.

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